SEED AND FRUIT CHARACTERS IN SELECTED SPERMACOCEAE AND COMPARISON WITH HEDYOTIDEAE (RUBIACEAE)

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ABSTRACT

Seed and fruit morphology of ten species of five American genera of Spermacoceae (*Diodia, Ernodea, Mitracarpus, Richardia, Spermacoce*) are described, illustrated, and compared with that in the Hedyotideae. These data support the taxonomic recognition of two distinct tribes.

RESUMEN

La morfología de la semilla y del fruto de diez especies de cinco géneros americanos de Spermacoceae se describe, se ilustra, y se compara con la de Hedyotideae. Estos datos apoyan el reconocimiento taxonómico de dos tribus distintas.

INTRODUCTION

Seed morphology in *Houstonia* L. and related genera in the tribe Hedyotideae Cham. & Schltdl. ex DC. (Rubiaceae) has contributed valuable information, especially when combined with data from chromosome number and pollen structure (Terrell et al. 1986; Terrell 1996). More recent taxonomic studies have continued to emphasize the importance of seed data (Terrell 2001a, 2001b, 2001c).

This study investigates the morphology of the seeds and fruits in selected genera in the tribe Spermacoceae Bercht. & J. Presl. We contrast this information with previously acquired seed data for the Hedyotideae. The two tribes include some superficially similar genera and species (e.g. *Oldenlandia* L. and *Spermacoce* L.), but structure and development of their fruits and seeds are fundamentally different and deserve further study. The Hedyotideae have few to many small seeds per locule, nearly always in subglobose biloculate capsules. In contrast, the fruits of Spermacoceae have one large seed per locule and are generally more structurally complex and vary considerably among the genera. Bremer and Manen (2000) expanded the tribe Spermacoceae to include the Hedyotideae; however, our data from seed and fruit morphology in five genera do not appear to support this inclusion.

Verdcourt (1958) proposed a classification of the Rubiaceae in which he recognized three subfamilies. The Rubioideae, the largest subfamily, contained 17 tribes including the Hedyotideae and Spermacoceae. Bremekamp (1966)

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modified Verdcourt's system and recognized eight subfamilies in the family and 19 tribes in the Rubioideae (including the Hedyotideae and Spermacoceae). Verdcourt (1976), still recognizing his original three subfamilies, reduced the number of tribes in the Rubioideae to 12 and maintained Hedyotideae and Spermacoceae. Robbrecht (1988, 1993) recognized four subfamilies and 19 tribes in subfamily Rubioideae. The latter included Hedyotideae and Spermacoceae.

MATERIALS AND METHODS

Scanning electron microscopy was employed in this study of seeds and fruits. The investigation was carried out at the Biology Department, University of South Florida, using a JEOL JSM-35 microscope operating at 15 kilovolts. Ten species in five genera were examined from herbarium material at the University of South Florida (USF) (Table 1). The species examined were those most readily available and representative of species native to tropical America, especially of the Caribbean basin. Tables 1 and 2 provide nomenclatural author's names.

RESULTS

The Spermacoceae is a pantropical tribe that may consist of as many as 19 genera and 450 species. Its generic delimitations are a matter of dispute. Eleven currently recognized genera native to the New World are summarized in Table 2. Morphological characters of the seeds and fruits of five genera of Spermacoceae native to the Americas are described as follows:

Diodia: Ovary 2(3–4)-locular; ovules solitary in each locule, attached to the middle of the septum. Fruit with 2(3–4) indehiscent mericarps, these fleshy or dry capsules. Seed enclosed within the hardened mericarp (accessible only by dissection), oblong, somewhat compressed, the dorsal surface convex, the ventral surface with a slightly sunken, central, longitudinal groove (see comments in Discussion), the testa finely reticulate (Fig. 1A–D).

Ernodea: Ovary 2-locular; ovules solitary in each locule, attached to the middle of the septum. Fruit fleshy, oblong, becoming hardened in drying, not easily separated into indehiscent mericarps (accessible only by dissection). Seeds oblong, somewhat compressed, the dorsal surface convex, the ventral surface with a slightly sunken, central, longitudinal groove, the testa finely reticulate (Fig. 3C,D)

Mitracarpus: Ovary 2(3–4)-locular, ovules solitary in each locule, attached near the middle of the septum. Fruit a thin-walled circumscissile capsule, the distal portion falling away with the calyx limb, the septum usually persistent. Seed oblong to globose, the dorsal surface convex, the ventral face divided into 4 distinct areas by an x-shaped groove, the testa finely reticulate (Fig. 3A,B).

Richardia: Ovary (2–)3–4(–6)-locular, ovules solitary in each locule, attached near the middle of the septum. Fruit dehiscing into dry mericarps, the ventral mericarp face with either a medial keel or narrow groove. Seed filling

Table 1. List of species and collections examined for this study.

Species	**Source/Voucher Information**
Diodia teres Walter	Florida. St. Johns Co.: *Hansen & Hansen 9844* (USF)
Diodia virginiana L.	Florida. Collier Co.: *Lakela 27450* (USF)
Ernodea littoralis Sw.	Florida. Monroe Co.: *Gann & Bradley 449* (USF)
Mitracarpus hirtus (L.) DC.	Florida. Lake Co.: *Daubenmire & Daubenmire s.n., 18 Oct 92* (USF)
Richardia brasiliensis Gomes	Florida. Hillsborough Co.: *Gregory 7* (USF)
Richardia humistrata (Cham. & Schltdl.) Schult. & Schult.f.	Florida. Escambia Co.: *Wilhelm & Burkhalter 7877 (USF)*
Richardia scabra L.	Florida. Hillsborough Co.: *Robinson s.n., 14 Jul 77* (USF)
Richardia tricocca (Torr. & A. Gray) Standl.	Mexico. Hidalgo: *Hernández M. & Vásquez 3466* (USF)
Spermacoce assurgens Ruiz & Pav.	Florida. Pinellas Co.: *Fleming 3862* (USF)
Spermacoce prostrata Aubl.	Florida. Collier Co.: *Lakela 31721* (USF)
Spermacoce tetraquetra A. Rich.	Florida. Miami-Dade Co.: *Bradley 1999* (USF)
Spermacoce verticillata L.	Florida. Dade Co.: *Avery 589a* (USF)

TABLE 2. Eleven currently recognized genera of Spermacoceae native to the Americas, the estimated number of species, native distribution, and reference to a recent taxonomic treatment.

Crusea Cham. & Schltdl. 13 spp.	southwestern U.S., Mexico; Anderson 1972.
Diodia L. 5 spp.	North America, Mexico, Central America, West Indies, and South America; Bacigalupo & Cabral 1999.
Emmeorhiza Pohl ex Endl. 1 sp.	Brazil.
Ernodea Sw. 4 spp.	Florida, West Indies, Belize, Honduras, and Guatemala; Negron-Ortiz and Hickey 1997.
Galianthe Griseb. ca. 50 spp.	Central America and South America; Cabral 1991.
Mitracarpus Zucc. ca. 30 spp.	Mexico, Central America, and South America.
Psyllocarpus Mart. & Zucc. 8 spp.	Brazil; Kirkbride 1979.
Richardia L. 15 spp.;	Mexico, Central America, South America; Lewis and Oliver 1974.
Scandentia E.L. Cabral & Bacigalupo. 4 spp.	Brazil; Cabral & Bacigalupo 2001.
Spermacoce L. ca. 150 spp.	North America, Mexico, Central America, West Indies, and South America; [Including *Borreria* G. Mey.; *Hemidiodia* K. Schum.]
Staelia Cham. & Schltdl. 15 spp.	Brazil.

the mericarp tightly (sect. *Richardia*) or slightly smaller than the mericarp (sect. *Asterophyton (K.Schum.)* W.H.Lewis & R.L.Oliv.), oblong or broadly ovate, the dorsal surface convex, the ventral surface with a slightly sunken, central, longitudinal groove, the testa finely reticulate (Fig. 3E,F;4A-F)).

Spermacoce: Ovary usually 2-locular, ovule solitary in each locule. Fruit

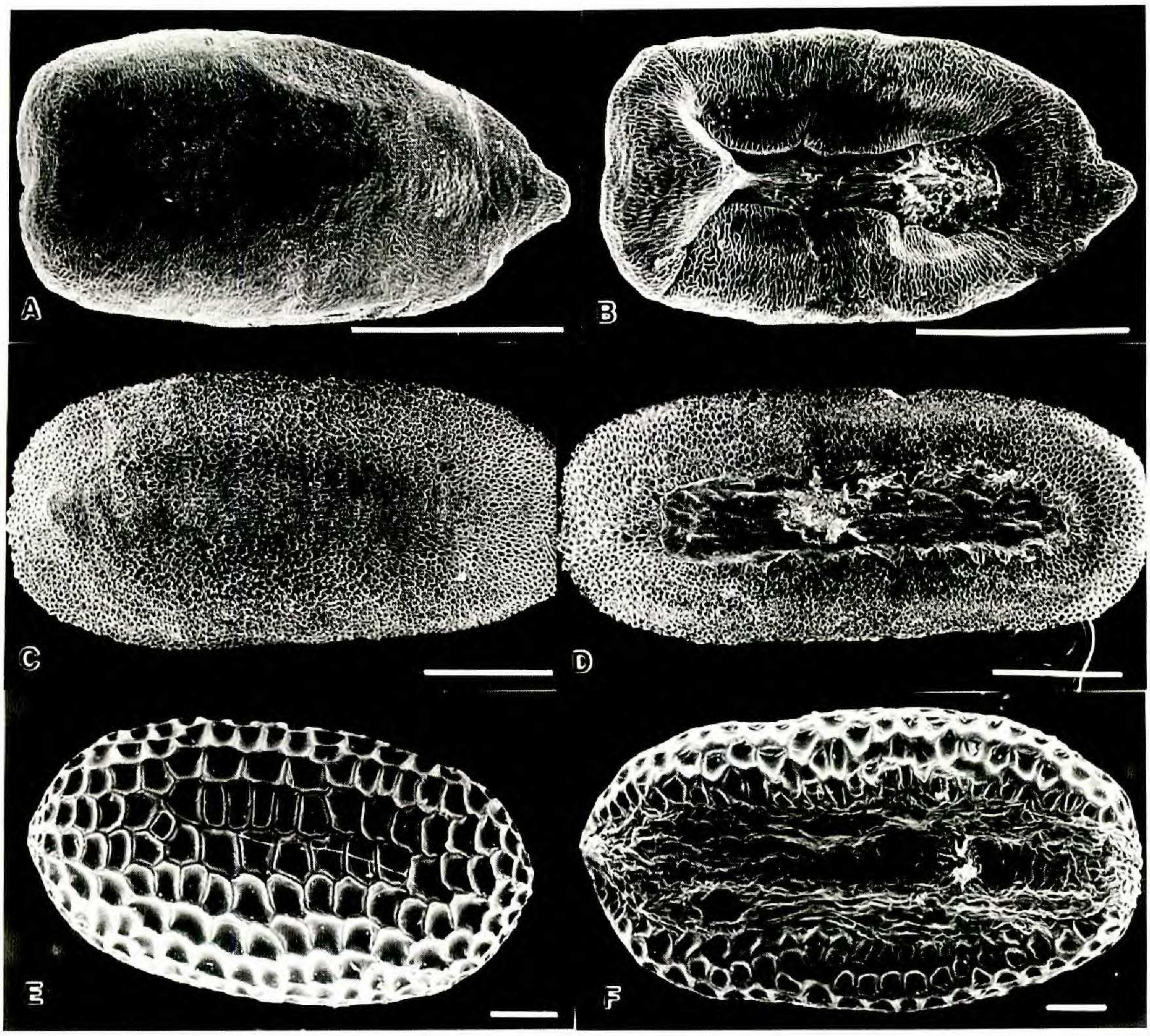

Fig. 1. Dorsal and ventral views of seeds examined by SEM. *Diodia teres* (A–B), *D. virginiana* (C–D), *Spermacoce prostrata* (E–F). Scale bars are 1000 microns (A–B), 100 microns (C–F). Sources of collections listed in Table 1.

dehiscing into 2 mericarps, both opening to release the seed (sect. *Borreria* (G. Mey.) Verdc.) or one mericarp opening to release the seed while the other remains closed by a fragile, easily removable septum (sect. *Spermacoce*). Seeds are ellipsoidal, ovoid, or oblong, the dorsal surface convex, the ventral surface with a slightly sunken, longitudinal groove extending to the ends, this sometimes with small elaiosomes, the testa reticulate (Fig. 1E,F; 2A–F).

DISCUSSION

Some workers continue to treat *Spermacoce* in the broad sense, while others divide it into several genera. *Borreria* is treated either as a separate genus or as a section of *Spermacoce* based on fruit dehiscence (capsule with both carpels opening to release the seeds in *Borreria* or a capsule with 1 carpel opening to release the seed and 1 remaining closed). Based on our study of seed morphology, *Borreria* does not appear to warrant recognition as a genus. Recently,

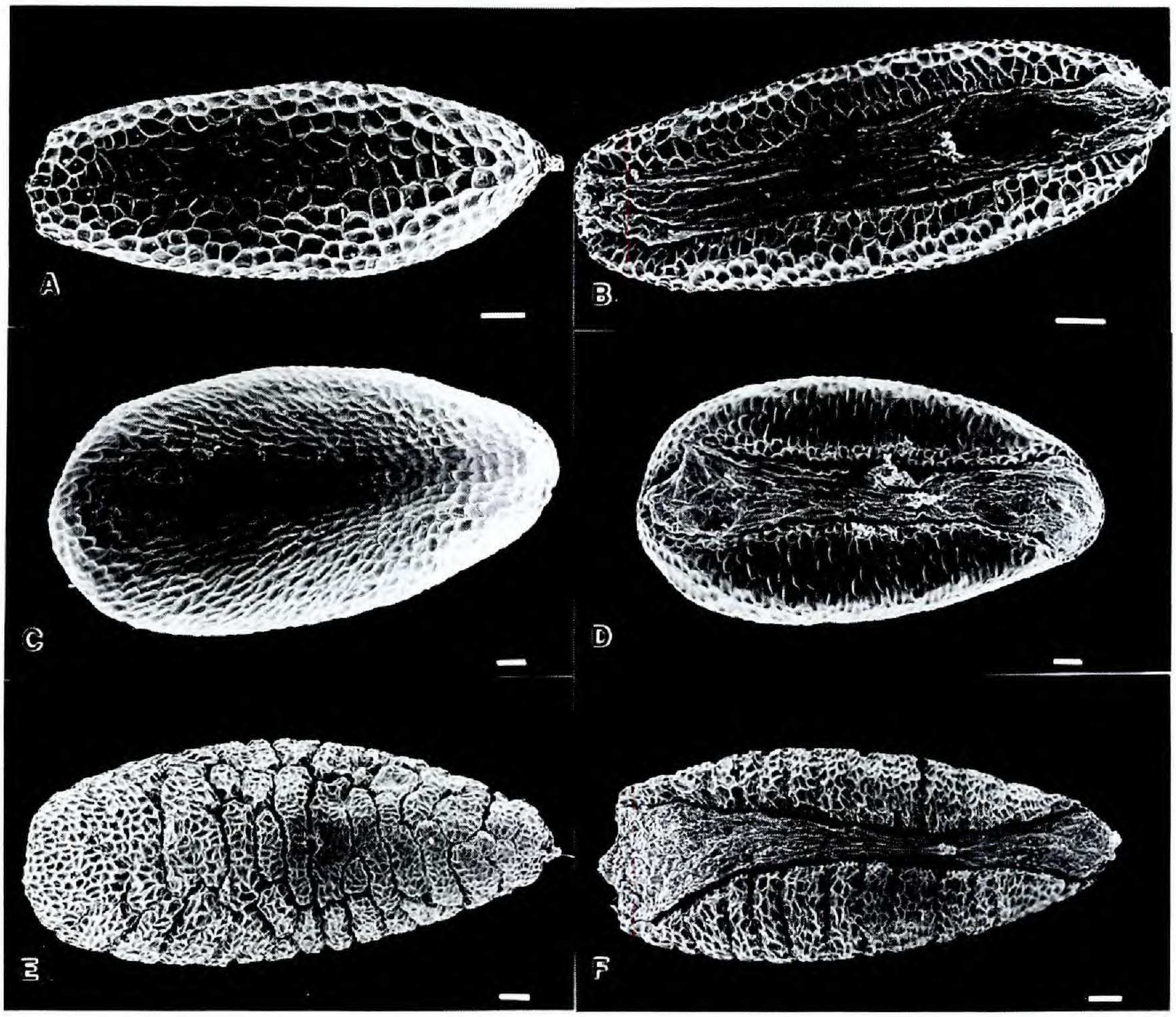

Fig. 2. Dorsal and ventral views of seeds examined by SEM. ***Spermacoce verticillata*** **(A–B),** ***S. tetraquetra*** **(C–D),** ***S. assurgens*** **(E–F). Scale bars are 100 microns. Sources of collections listed in Table 1.**

Galianthe was resurrected as a segregate genus from *Borreria* (Cabral 1991) and *Scandentia* was described (Cabral & Bacigalupo 2001). Both *Galianthe* and *Scandentia* are distinguished from *Borreria* primarily in habit with more or less lax, thyrsoid, apical inflorescences in contrast to the congested, apical and/or axially glomeruliform inflorescences of *Borreria* s. str. *Emmeorhiza*, a monotypic South American genus closely related to *Borreria*, *Galianthe*, and *Scandentia* has an umbelliform inflorescence. The seeds of *Spermacoce assurgens*, *S. prostrata*, and *S. verticillata*, which would be placed in *Borreria* on the basis of fruit dehiscence, do not differ significantly from that of *S. tetraquetra* traditionally placed in *Spermacoce* (Fig. 1E,F; 2A–F). Further work on the *Spermacoce* complex is needed and is underway by various other workers (e.g., E.L. Cabral, N.M. Bacigalupo, and S. Dessein).

Diodia also presents similar problems in circumscription. *Hemidiodia*, a monotypic genus with 2 indehiscent mericarps and long considered closely related to *Diodia*, was transferred to *Borreria* subg. *Dasycephala* (DC.)

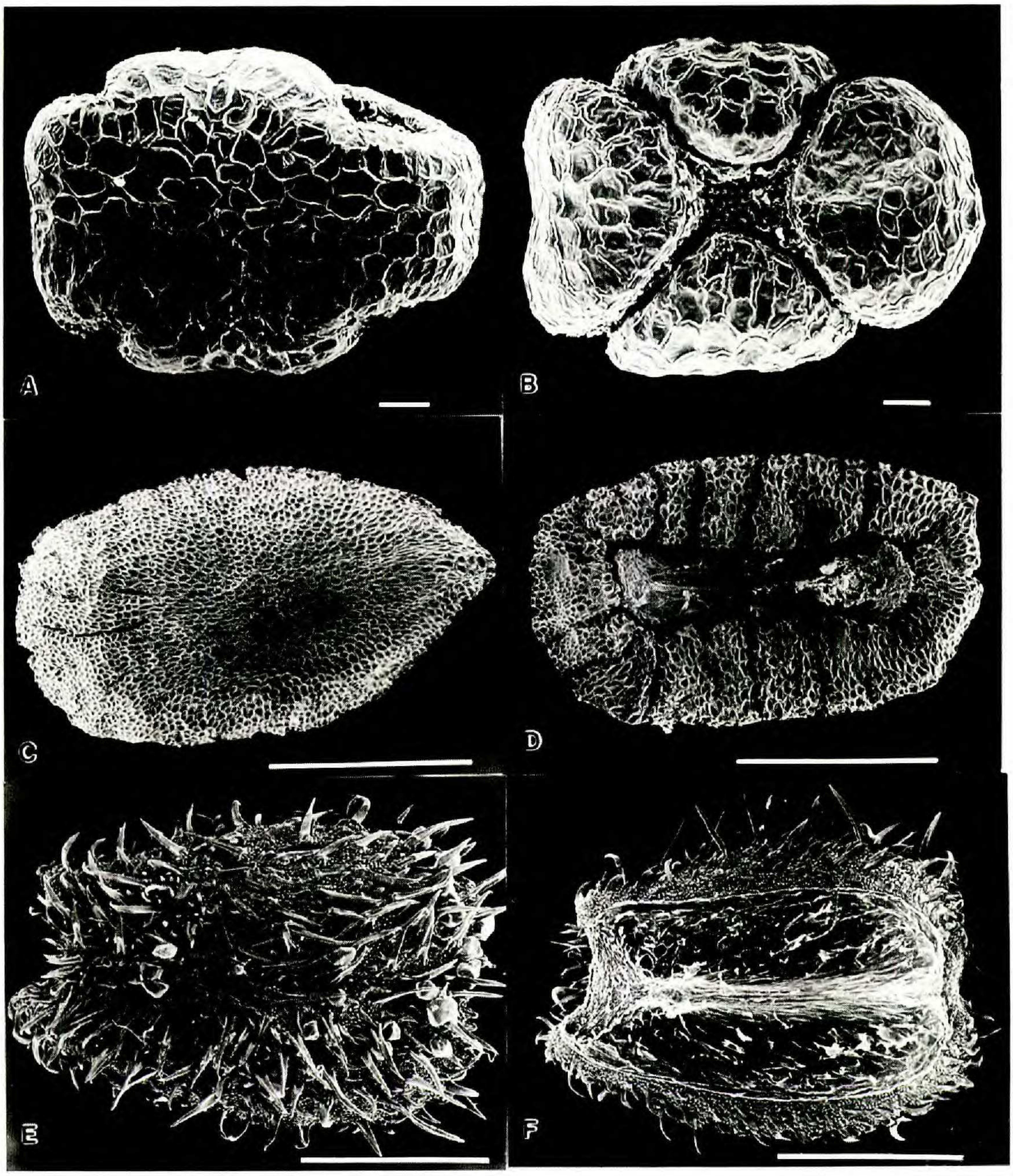

Fig. 3. Dorsal and ventral views of seeds and mericarps examined by SEM. *Mitrocarpus hirtus* seeds (**A–B**), *Ernodea littoralis* seeds (**C–D**), *Richardia brasiliensis* mericarps (**E–F**). Scale bars are 100 microns (A–B), 1000 microns (C–F). Sources of collections listed in Table 1.

Bacigalupo & E.L.Cabral by Bacigalupo and Cabral (1996). Another study by Bacigalupo and Cabral (1999) defined *Diodia* as comprised of only five American species; the other species previously referred to the genus are transferred to *Galianthe* or *Borreria*. These workers exclude *Diodia teres* and related species from *Diodia* s. str. The placement of these species is still under study by Bacigalupo and Cabral. The seed morphology is markedly different between the two southeastern U.S. species, *Diodia virginiana* and *Diodia teres*, examined in this study (Fig. 1A–D). The seed of *D. virginiana* is oblong with an equally rounded apex and base. The testa has more or less isodiametric cells. In contrast, that of *D. teres* is oblong with an apical projection and a truncate base. On the ventral surface, the base and sides are somewhat enrolled onto the longitudinal groove. The cells of the testa surface are elongate (2–3 times as long as wide). Further study by other workers may prove *D. teres* and related species to be distinct at the generic or subgeneric level.

The seeds of the four *Richardia* species examined are fairly uniform, differ only slightly in size and shape, and the genus appears to be a natural assemblage.

Ernodea seeds and fruits are most similar to those of *Diodia virginiana*.

The seeds of *Mitracarpus* are unique among those examined in this study. The distinct x-shaped groove and the circumscissile dehiscent capsule, both features unique in the tribe, suggest that it may be a distinct subtribe.

The Hedyotideae is much simpler in seed morphology than is the Spermacoceae, but has much more variation in seed shape and size. The seeds are typically in subglobose capsules, each bearing few to many seeds borne on complexly structured placentas. The variation shown by the seeds of the various taxa is very great and each genus, subgenus, or section often has its own particular seed shape. The following are some examples of seed diversity found in the Hedyotideae: (1) *Houstonia* L. has crateriform seeds, each with a ventral subglobose cavity (subg. *Houstonia*) or with a hilar ridge in a ventral shallow depression (subg. *Chamisme* Raf. sect. *Amphiotis* (DC.) Terrell) or with a hilar ridge in a ventral boat- or cup-shaped depression and with other complex structure (subg. *Chamisme* sect. *Ericotis* (Terrell) Terrell) (Terrell et al. 1986, Terrell 1996); (2) *Oldenlandia* L. typically has very small trigonous seeds, 50–100 or more per capsule (Terrell 1996); (3) the *Hedyotis fruticosa* L. group has dorsiventrally compressed seeds with a short to long raised hilar ridge (Terrell 1996); and (4) *Stenotis* Terrell and *Stenaria* (Raf.) Terrell have ellipsoid seeds with a central punctiform hilum (Terrell 2001a, 2001b).

The Spermacoceae, in contrast, have one seed per locule, and the locules develop into varied mericarps. The complexity occurs in the mericarps as well as in the seeds; the seeds examined here do not seem to exhibit much variation, although the *Mitracarpus* seed is an exception. In the Spermacoceae, some mericarps are hardened and indehiscent (e.g., *Diodia*), others are fleshy (*Ernodea*), and some open widely (e.g., *Spermacoce*). Each genus often has its characteristic kind of mericarp, and its structure is important in classification (e.g., *Richardia*, Fig. 4A,B). The mericarps may be more important in classification than the seeds (e.g., our figures show the similarity of seeds among the various genera). The presence of such varied mericarps contrasts with the morphology of the Hedyotideae, which have no such seed covering, just the bare seeds attached to a multi-branched placenta.

An additional seed feature not found in the Hedyotideae is the ventral

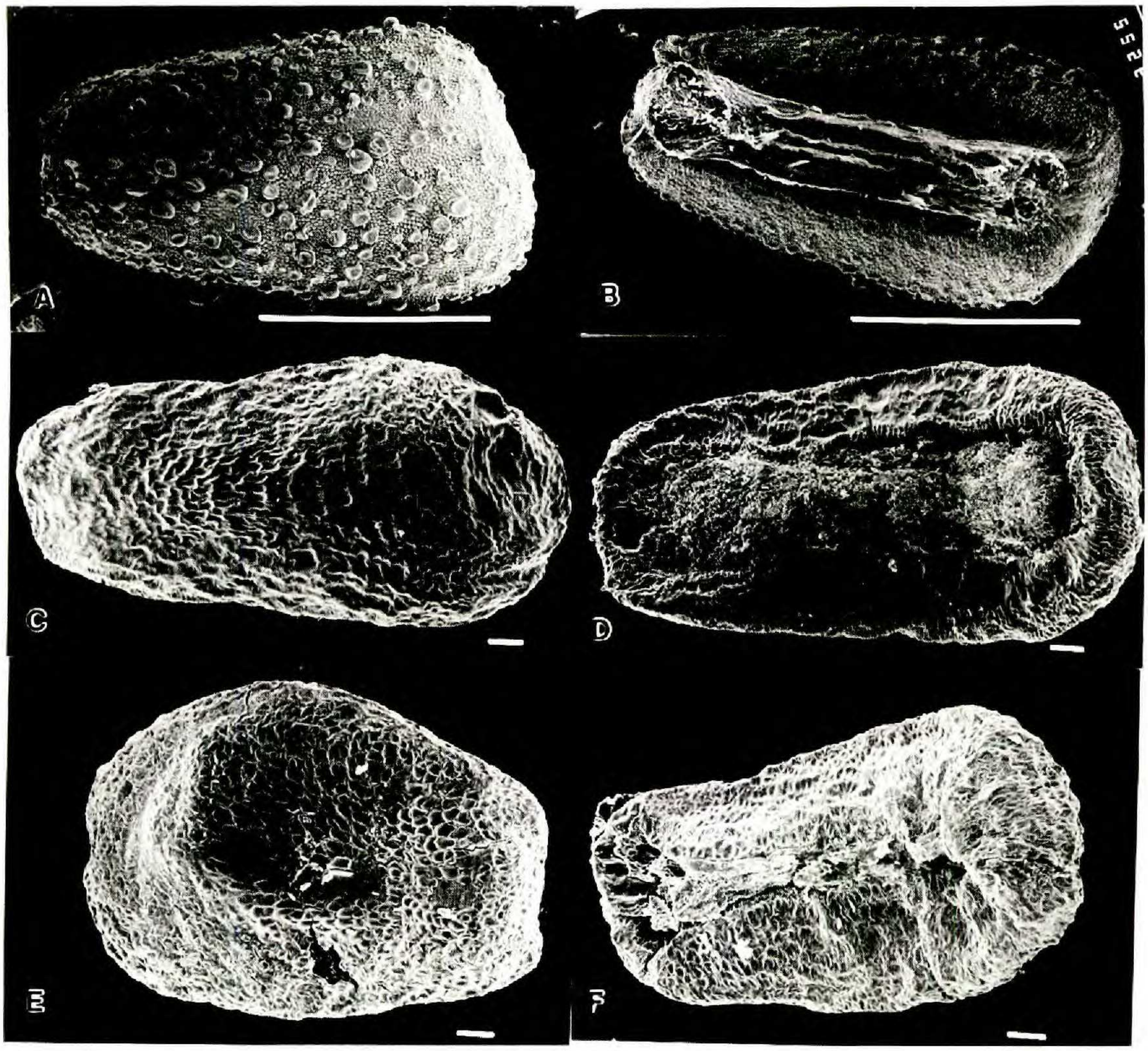

Fig. 4. Dorsal and ventral views of seeds and mericarps examined by SEM. *Richardia scabra* mericarps (**A–B**), *R. humistrata* seeds (**C–D**) and *R. tricocca* seeds (**E–F**). Scale bars are 1000 microns (A–B), 100 microns (C–F). Sources of collections listed in Table 1.

(adaxial) longitudinal groove which resembles a raphe. This structure was designated as a strophiole by Kirkbride (1979), Bacigalupo and Cabral (1996), and other South American botanists. The structure and terminology of this apparent raphe needs further study. It occurs on all seeds of Spermacoceae that we have examined. The Hedyotideae differ in having a so-called hilum, a punctiform scar or a more elongated ridge-top scar on the seed.

Although our evidence from five selected genera represents a limited survey of the possibly 19 genera of Spermacoceae, it is sufficient to lead us to seriously question the union of the Spermacoceae and Hedyotideae.

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